Linking plant hydraulics and beta diversity in tropical forests

Title: Bridging the gap between plant hydraulics and beta diversity in tropical forests

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Key words: trait-mediated environmental filtering, plant-water relations, ecohydrology, drought, xylem anatomy, safety-efficiency trade-off

Introduction

In tropical forests, studies of xylem traits governing water transport through plants, or hydraulic architecture (HA) (Tyree *et al.*, 1991), and the turnover of species along environmental gradients (Gentry, 1988), or beta-diversity (sensu Ackerly & Cornwell, 2007), have progressed mostly in parallel until recently (Hao *et al.*, 2008; Bartlett *et al.*, 2015). In this Issue of *New Phytologist*, Cosme et al. (2017) present a timely contribution to the intersection of plant hydraulics with trait-based community ecology. Building on previous biogeographical work which demonstrated high species turnover (beta-diversity) across a gradient from valleys to plateaus in central Amazonia (Schietti *et al.*, 2014), they explore how variation in HA might underpin this sorting, sampling pairs of congeneric species restricted mostly to either plateau or valley habitats. Valley species had significantly lower wood density and higher hydraulically-weighted vessel diameter and vessel area, while the relationships of vessel diameter and the leaf:sapwood area ratio with tree height demonstrated differences in the two habitats. This is notable, as it suggests that species differentiation in water transport traits mediate edaphic filtering along the valley-to-plateau gradient, in contrast to previous work where wood mechanical support mediated valley-to-plateau environmental filtering (Fortunel *et al.*, 2014). The 'hydro-edaphic gradient' (as Cosme et al. 2017 describe it) is a pervasive feature of many tropical forests (and in particular, Amazonia; see (Nobre *et al.*, 2011)), but is often overlooked in ecosystem models and studies of ecosystem processes in this biome (de Gonçalves *et al.*, 2013). If plant HA traits mediate the environmental filtering of species at this local scale, as the findings of Cosme et al. suggest – and given the projection by climate models towards an increased frequency of drought events or overall seasonality in precipitation seasonality (stronger dry seasons and wet seasons (Boisier *et al.*, 2015)) – then this background edaphic gradient could be further amplified and thus lead to an even stronger trait-mediated sorting of species under climate change.

Habitat Favourability, Durational Stability, and the Safety-Efficiency Trade-off

Two main concepts that underpin trait-mediated environmental filtering as presented in Cosme et al. (2017) are: *1)* the habitat as defined by hydro-edaphic conditions and as a template upon which various ecological strategies are derived; and *2)* a trade-off in xylem safety and efficiency defining the range in ecological strategies operating on top of this habitat template. Both of these concepts have a rich

history and it is useful to explore them briefly. First, the notion of a habitat as a set of environmental and ecological conditions defining a space occupied by an organism has been around for centuries. It was arguably Southwood's (1977) treatise 40 years ago on the 'habitat templet' that was the first rigorous attempt at quantifying habitat along the two axes of general 'favourableness' and 'durational stability'. Understanding plateau and valley habitats in tropical forests in terms of their favourableness and durational stability raises important questions in light of the results presented by Cosme et al (2017), explored below.

Second, it has been thought for some time that the ability of a plant to resist a meaningful degree of moisture stress (hydraulic safety) would come at the cost of reduced maximum potential rate of water transport in xylem (hydraulic efficiency). It turns out that both the expectation of and evidence for such a trade-off (or lack thereof) is quite complex and mixed, especially when considering a range of scales within plant xylem at which safety and efficiency operate (see Bittencourt *et al.*, 2016; Gleason *et al.*, 2016 and references therein). Nonetheless, Cosme et al. (2017) observed shifts towards wider vessels, deeper sapwood, and lower wood density in valley habitats, all of which are consistent with the hypothesis that these species prioritize efficiency, in contrast to species in plateau habitats, which prioritize safety. Given the complexities surrounding the safety-efficiency trade-off in plant xylem, it is remarkable that such distinct plant strategies emerged in these contrasting habitats.

However, the safety-efficiency trade-off interpretation of these patterns in vessel traits is contingent on both: a) increasing distance to the water table acting as a suitable proxy for the degree of hydraulic stress; and b) the various vessel traits (in particular vessel diameter and frequency) acting as suitable proxies for both efficiency and safety. (Cosme et al. (2017) did not measure xylem hydraulic conductivity or the xylem pressure at which a meaningful amount of efficiency is lost directly, but highlight these measures as priorities for future work). Exceptions to these two assumptions are worth considering.

As Cosme et al. (2017) acknowledge, there is the likelihood of stress induced by hypoxia or anoxia during periods of waterlogging in the wet season in valley habitats; hence maxima, and not minima, in soil hydraulic conditions could also be a (non-mutually exclusive) filtering mechanism. Consistent with this hypothesis, 90% of the species turnover from valley to plateau habitats occurs in areas affected by seasonal water table fluctuations (i.e., closer to valley bottoms; Schietti *et al.*, 2014). It is also possible that in valley habitats, a shallow rooting habit (due to the avoidance of waterlogging) combined with small reductions in the water table and rapid drainage of sandy soils during inter-storm periods of the dry season, albeit brief, could induce dramatic declines in soil water potential. In this case, another (again, not mutually exclusive) explanation for lower density wood and deeper sapwood in these valley habitats is to promote water storage via greater hydraulic capacitance to sustain transpiration during these short periods of potentially limiting soil moisture availability (Borchert & Pockman, 2005). While the clay-rich soils of some Amazonian plateau habitats have a large fraction of water that is tightly bound and thus unavailable to plants (Fisher *et al.*, 2008), the greater distance to the water table likely contributes to a much deeper rooting profile, and hence the large volume of soil available to plants via deep rooting (Nepstad *et al.*, 1994), which could allow for more favourable conditions in plateaus versus valleys during droughts. Consistent with this, drought conditions in Borneo disproportionately affected species adapted to wet habitats, but the exact mechanism for this is not yet fully resolved (Itoh *et al.*, 2012). Cosme et al. (2017) have indeed highlighted that valley habitats are "…very hydrologically dynamic" and, as a counter-example to a rigid trade-off in safety versus efficiency, that valley species likely maintain a reasonable degree of safety by modulating efficiency *at a scale different* from that at

which safety is maintained. In these species, increased efficiency arose primarily via increased sapwood area (individual scale), while the maintenance of safety purportedly occurred by maintaining a network of not-too-large vessels (tissue scale), as mean vessel diameter and vessel density did not differ significantly between plateau and valley species. The same mechanism, in which safety and efficiency can be effectively manipulated at different scales, can be said to be true for plateau species, and highlights the importance of a network-scale view of plant xylem (Loepfe *et al.*, 2007). In sum, the complexities of hydro-edaphic conditions in valley versus plateau habitats manifest themselves in orthogonal dimensions -- both overall favourability as well as in durational stability (or extremes), and these dimensions comprise contrasting templates upon which hydraulic safety and efficiency are presumably maximized.

Using measurements and models to discern causes and consequences of trait-mediated environmental filtering

There is immense value in the findings of Cosme et al. (2017), as is the case for other similarly designed studies (Hao *et al.*, 2008; Fortunel *et al.*, 2014). First, the strong evidence presented for filtering by the hydro-edaphic habitat in terms of HA traits suggests the need for measurements designed to probe the chain of mechanisms which link xylem anatomy to plant hydraulic traits, and in turn, to plant performance in contrasting habitats, which could be said to be the 'Holy Grail' of a trait-based community ecology in terms of plant-water relations. Specifically, augmenting these findings with *in situ* measures of sap flux, tissue water content and/or potential, stem growth and leaf phenology in these contrasting congeneric species and habitats over periods of regular (seasonal) as well as extreme (e.g., drought and/or flooding) variability in soil water availability would go far towards achieving this goal. Second, there is exceptional value for the development of ecosystem models, particularly those which eschew traditional approaches involving an *a priori*-defined biogeographic range for a given plant type, and instead seek to represent ecosystem response to environmental change as an emergent outcome of trait-mediated environmental filtering (Fisher *et al.*, 2015). The identification by Cosme et al. (2017) of plant hydraulic strategies can inform models which are now capable of incorporating plant hydraulic traits and the ecosystem-level outcome of community-level variation in these traits (Christoffersen *et al.*, 2016). Combining these empirical and modelling efforts will be invaluable in advancing our understanding of both plant response to environmental change and effect on ecosystem function, respectively (Lavorel & Garnier, 2002).

Acknowledgements

BOC acknowledges support from the Next-Generation Ecosystem Experiments (NGEE-Tropics) project, funded by the U.S. Department of Energy, Office of Biological and Environmental Research. Patrick Meir acknowledges support from NE/J011002/1 (NERC, UK) and FT110100457 and DP170104091 (ARC, Australia).

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